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Types of *Copepoda* and *Drepanidotaenia lanceolata* (Bloch) host-parasite systems established experimentally

Typy układów żywiciel-pasożyt — *Copepoda* i larwy *Drepanidotaenia lanceolata* (Bloch), wyróżnione eksperymentalnie

Attemps have been made for a long time in parasitology to classify hosts from the point of view of conditions which they create for the parasites living in them. Terms like principal host, obligatory host, auxiliary host, accidental host, reserve host, etc. have already been widely accepted.

The above terms and descriptions refer to physiological, ecological, zoogeographical, topographical and a number of other phenomena. Davtian et Šulc (1954) made an attempt at systematizing the nomenclature and establishing some general host groups, and even some types of „host-parasite" systems in helminthology. They established four categories of „host-parasite" systems, with the conditions and development stage of the parasite in the organism of the host accepted as the main criterion. This criterion is not adequate, particularly if it is to be applied, as the authors want it to be, to all parasitic worms, since their development cycles are in many cases very complex and consequently, the relation and interdependence of hosts and parasittes in various periods of their development are very complicated. The above conclusion is drawn on the basis of detailed investigations into definite species and development forms of parasites and their hosts. During his research on the larvae of *Triaenophorus lucii* (Müll.) and their hosts *(Copepoda)*, Michajłow (1932) distinguished five host groups of the larvae. He also showed that the formation of a „larva-copepode" system in *Triaenophorus lucii* depends on two definite selection barriers, viz. (1) the host's digestive juices, and (2) the conditions prevailing in its body cavity. Thus, in addition to the criterion accepted by Davtian

and Šulc, 1954 (the conditions of the development of the parastite in the organism of the host) it is indispensable to accept another criterion, i.e. the resistane of the larvae to the action of the digestive juices of the host.

It seems then that it is precisely detailed investigations into various species and various development forms of parasites and their hosts, conducted from the point of view the variety of relations that may exist between them, that will supply a basis for more general conclusions on types of „host-parasite" systems.

The present paper is an attempt at classifying „host-parasite" systems on the basis of the example supplied by *Drepanidotaenia lanceolata* (Bloch) larvae and their intermediate hosts (*Copepoda*). We drew on the work of Davtian and Šulc (1954) for what appeared to us to be correct — (a) the classification was applied to types of „host-parasite" systems and not to hosts only, and (b) a set of terms was used to distinguish warious types of these systems. It seems justified to use certain terms here as it is easier to associate them with a given type of system each, and because they constitute their succinct definitions as it were. While adopting the terms for the types of „host-parasite" sysems established by us we tried to take into account the already existing ones (with one exeption) so as not toi lengthen their already long list.

Material and methods

Adult *D. lanceolata* specimens were obtained from (a) post-mortems of their final hosts (*Anser anser dom.*), (b) removal of worms from their hosts. The post-mortems were made at the poultry slaughter-houses at Płock (1954) and Lublin (1955—56). Worms were removed with the help of hydrobromide arecoline from geese at the Żukówek farm, Nocpolsk PGR near Płońsk and from some bred near Grójec (1956—57). A total of 534 geese were examined.

Plankton was caught in bodies of water near Warsaw (clay pits near Szczęśliwice and in Wola, Lake Czerniakowskie, some bodies of water in the Kampinos Forest), in peat-hags at the Nacpolsk PGR (State Farm) and in pools near Grójec. The catches were made with a plankton net in various months from September 1954 to June 1957.

A total of 2,053 crustaceans of 18 species coming from the above mentioned bodies of water were examined. Four of the species (*Diaptomus vulgaris* Schmeil, *Diaptomus gracilis* G. O. Sars, *Cypridopsis* sp. and *Daphnia* sp.) did not get invaded

at all. The species subject to invasion are referred to below in this paper. The nomenclature applied to *Copepoda* was based on the paper of Rylov (1948).

The method of individual host culture (Michajłow, 1953; Kisielewska, 1955—56) was used in the experiments.

In order to interpret the phenomena observed in the development of larvae of various host species exclusively from the point of view of the variability of „host-parasite" systems, it was necessary to limit as far as possible the influence of additional factors (e. g. the influence of the environment of the second order) which might modify in a certain degree the course of the invasion and the development of the larvae. Consequently (a) *D. lanceolata* eggs were used for invasions which had stayed in water not longer than 5 to 6 days after they were squeezed out of the proglottids and thus constituted an invasional material of full value (Kisielewska, 1958), (b) these eggs were kept at room temperature with light and oxygen reaching them, since it had proved that lack of these factors told on the vitality of the oncospheres (Kisielewska, 1958), (c) the contact time of cyclopes and the parasite's eggs was about 24 hours, (d) the invaded cyclopes were kept in the same conditions (as regards water in cultures, size of test tubes, composition of vegetation, temperature and light), (e) the results were interpreted for each season separately (Kisielewska, 1957, a).

Types of „*D. lanceolata* larvae — *Copepoda*" systems and criteria for their distinction

Intermediate hosts of *D. lanceolata* have been frequently mentioned in literature: Thus, Rossefer (1890) recorded the finding of the cercocysts of this tapeworm in *Cyclops serrulatus* and *Cyclops globosus;* Daday (1901) discovered cercocysts of the same tapeworm species in *Diaptomus spinosus* Dad., and Potiomkina (1938) in *Cyclops diaphanus, C. leuckarti, C. albidus, C. oithonoides, C. viridis,* Ruszkowski (1932) succeeded in invading experimentally *Cyclops strenuus* and *Diaptomus gracilis* (the latter to a small extent) with *D. lanceolata* eggs, and Potiomkina (1938) obtained invasions in *Cyclops strenuus* (90%), *C. leuckarti* (80%) and *C. oithonoides* (80%). The list of the intermediate hosts of *D. lanceolata* should also include the following species: *Cyclops speratus* and *C. insignis* (according to Skrjabin et Mathe-

Table I

Extensity and intensity of invasion, speed and course of development of *D. lanceolata* larvae in hosts

Host species	Autumn (IX—XI)								Winter (XII—II)					
	Sex	Age	No. of examined	%	Intensity limit	Intensity aver.	Speed of develop.	Course of development	No. of examined	%	Intensity limit	Intensity aver.	Speed of develop.	Course of development
Cyclops strenuus strenuus Fischer	♀	ad.	58	100	3—14	8.1	10—12	deg. present	48	56.3	2—15	9.4	10—19	deg. present
	♂	ad.	73	100	2—16	7.4	11—14	deg. present	27	100	3—14	8.1	10—17	deg. not stated
	—	Cop. IV, V	259	62,3	1—16	5,2	11—17	deg. present	21	59.6	10—13	11.3	12—15	deg. present
	—	Cop. III	—	—	—	—	—	—	9	66.7	2—5	3.1	14—19	deg. not stated
Cyclops vicinus Uljan.	♀	ad.	—	—	—	—	—	—	21	15.3	1—11	4.7	lack of data	deg. almost total
Cyclops furcifer Claus	♀	ad.	—	—	—	—	—	—	—	—	—	—	—	—
Mesocyclops leuckarti Claus	♀	ad.	—	—	—	—	—	—	8	6 inv.	4—16	9.2	11—13	lack of degen.
Macrocyclops fuscus (Jurine)	♀	ad.	3	2 inv.	2—3	2.5	lack of data	deg. present	7	5 inv.	1—2	1.7	lack of data	deg. present
Macrocyclops albidus (Jurine)	♀	ad.	6	4 inv.	1—10	4.8	10—15	deg. present	66	12,1	2—8	4.7	11—14	deg. present
	♂	ad.	7	5 inv.	2—10	6.1	10—15	deg. present	34	67.6	1—12	5.8	11—14	deg. rare
	—	Cop.	3	3 inv.	2—14	6.9	10—15	lack of deg.	6	4 inv.	4—9	6.1	11—14	lack of deg.

Acanthocyclops viridis Jurine	♀	ad.	14	34.7	1—8	3.2	12—14	deg. present	97	9.6	1—6	2.1	—	deg. total
	♂	ad.	—	—	—	—	—	—	74	81.7	1—14	5.2	16—19	deg. sporad.
	—	Cop.	—	—	—	—	—	—	6	4 inv.	1—2	1.4	18—23	deg. present
Acanthocyclops bicuspidatus (Claus)	♀	ad.	—	—	—	—	—	—	9	7 inv.	4—9	5.8	16—20	lack of deg.
	—	Cop.	—	—	—	—	—	—	—	—	—	—	—	—
Acanthocyclops vernalis Fischer	♀	ad.	—	—	—	—	—	—	—	—	—	—	—	—
Eucyclops serrulatus s. str. Fischer	♀	ad.	58	24.1	1—12	5.7	12—13	deg. present	91	45.1	1—9	5.3	15—18	deg. present
Eucyclops speratus (Lillieb.)	♀	ad.	—	—	—	—	—	—	12	66.7	5—9	7.1	18—27	checked
	♂	ad.	—	—	—	—	—	—	7	6 inv.	4—7	6.3	23—34	checked
Eucyclops macrurus G. O. Sars	♀	ad.	4	4 inv.	1—10	4.1	lack of data	deg. present	28	17.8	1—6	2.3	16—24	deg. present
Eucyclops macruroides (Lillieb.)	♀	ad.	138	5.8	1—4	2.5	14—17	deg. present	60	49.9	1—8	2.4	12—15	deg. present

Table Ia

Extensity and intensity of invasion, speed and course of development of *D. lanceolata* larvae in hosts

Host species	Spring (III—V)								Summer (VI—VIII)					
	Sex	Age	No. of examined	%	Intensity limit	Intensity aver.	Speed of develop.	Course of development	No. of examined	%	Intensity limit	Intensity aver.	Speed of develop.	Course of development
Cyclops strenuus strenuus Fischer	♀	ad.	79	100	7—32	19.7	8—11	lack of deg.	22	100	12—45	22.8	8—10	lack of deg.
	♂	ad.	64	100	3—51	21.2	8—11	lack of deg.	37	100	9—22	18.1	8—9	lack of deg.
	—	Cop. IV, V	65	100	2—21	16.3	9—11	lack of deg.	63	100	6—38	20.8	8—12	lack of deg.
	—	Cop. III	—	—	—	—	—	—	34	100	1—16	4.8	10—14	lack of deg.
Cyclops vicinus Uljan.	♀	ad.	11	10 inv.	1—8	3.5	11—20	almost total degeneration	—	—	—	—	—	—
Cyclops furcifer Claus	♀	ad.	2	2 inv.	3—7	—	—	total degen.	—	—	—	—	—	—
Mesocyclops leuckarti Claus	♀	ad.	16	93.5	6—20	13.8	9—12	lack of deg.	10	100	8—17	10.3	8—10	lack of deg.
Macrocyclops fuscus (Jurine)	♀	ad.	—	—	—	—	—	—	—	—	—	—	—	—
Macrocyclops albidus (Jurine)	♀	ad.	8	8 inv.	3—6	3.9	lack	deg. present	—	—	—	—	—	—
	♂	ad.	—	—	—	—	of	—	—	—	—	—	—	—
	—	Cop.	—	—	—	—	data	—	—	—	—	—	—	—

Acanthocyclops viridis Jurine	♀	ad.	27	87.1	3—17	7.8	10—12	deg. rare	31	41.9	1—7	3.5	9—12	lack of deg.
	♂	ad.	19	100	2—19	10.2	11—12	lack of deg.	22	86.3	3—10	6.6	9—12	lack of deg.
	—	Cop.	11	90.9	1—6	2.7	11—15	deg. present	14	100	11—16	12.7	9—12	lack of deg.
Acanthocyclops bicuspidatus (Claus)	♀	ad.	14	100	12—19	13.3	10—12	lack of deg.	7	7 inv.	11—22	16.8	9—10	lack of deg.
	—	Cop.	8	8 inv.	11—16	14.1	9—11	lack of deg.	—	—	—	—	—	—
Acanthocyclops vernalis Fischer	♀	ad.	—	—	—	—	—	—	17	5.7	2	—	lack of data	deg. present
Eucyclops serrulatus s. str. Fischer	♀	ad.	84	36.9	1—11	3.9	9—13	deg. present	29	31.0	1—8	4.9	10—12	deg. rare.
Eucyclops speratus (Lillieb.)	♀	ad.	—	—	—	—	—	—	—	—	—	—	—	—
	♂	ad.	—	—	—	—	—	—	—	—	—	—	—	—
Eucyclops macrurus G. O. Sars	♀	ad.	16	37.4	1—8	4.5	10—13	lack of deg.	—	—	—	—	—	—
Eucyclops macruroides (Lillieb.)	♀	ad.	—	—	—	—	—	—	—	—	—	—	—	—

vossian, 1945). Various *Copepoda* species used to be included in the list of the intermediate hosts of *D. lanceolata* on finding in their body cavity larvae of this tapeworm which got there either through natural or experimental invasions. However, the significance of various *Copepoda* species as a link in the life cycle of *D. lanceolata* was never closely examined.

During the few years (1954—57) of experimental research on the development of *D. lanceolata* larvae in various species of intermediate hosts (*Copepoda*) some distinct differences in the course of the invasion itself came to light, and also in the process of development of larvae in the body cavity of the host. These differences became a basis for establishing criteria of the distinction of a few types of mutual relations between *D. lanceolata* larvae and their hosts. The criteria were as follows:

(1) Extensity of invasion.

The extensity of invasion is a phenomenon which differs entirely in experimental conditions from what is observed in natural bodies of water. In a body of water in which the distribution of tapeworm eggs is never even, plankton does not stand the same chance of getting invaded and for this reason the same *Copepoda* species caught at various places in the same body of water may show great differences in the extensity of invasion. In experimental conditions each cyclops stands a chance of consuming a great number of eggs and the extensity is higher than in the field, and constitues a permanent feature of a given host species. The results however seem therefore to be oven more reliable since in optimum invasion conditions not all specimens get invaded and differences in the extensity of invasion among various host species are considerable. In our experiments the extensity of invasion in various species and in various seasons varied from a few to a hundred per cent (Table I). It must be stressed that the results of experimental investigation into the extensity of invasion may witness only to the potential capacity of a given species at large. If, e. g. *Cyclops strenuus strenuus* Fischer, examined in spring, gets invaded in a 100 per cent we may assume that each specimen of this species at large which gets into contact with the source of invasion in that season will get invaded. But *Cyclops vicinus* Ulj., whose extensity of invasion varies within a few per cent in experimental conditions in spring, probably does not play any part as a host at large.

(2) Intensity of invasion.

Inspite of equal chances of getting invaded, cyclopes invaded experimentally show great differences in the strength of larval populations in their body cavity. These differences are smaller within one host species than among various host species, this being particularly clear from an analysis of mean intensities (Table I). The intensity of invasion in laboratory conditions, which in obligatory hosts amounts to tens of larvae in the body cavity of a specimen, is not comparable with the same feature at large either, where usually one larva, or, less frequently, two or three are found in one host. As is shown by experimental investigations this strength of population is far below the potential capacity of some host species.

(3) The behaviour of larvae in the intestine of the host.

Observations were made on the behaviour of larvae in the intestine of various species of intermediate hosts. Cyclopes were observed after an hour's or half-an-hour's contact with *D. lanceolata* eggs. The behaviour of the larvae in the intestine of hosts of various species varied, which should probably be ascribed to a higher or lower resistance of these larvae to the digestive juices of various hosts.

In the intestine of some host species (e. g. *Cyclops strenuus strenuus* ♀♀, ♂♂, Cop. Cop. V and IV in spring and summer, *Mesocyclops leuckarti* ♀♀ in spring, *Acanthocyclops bicuspidatus* ♀♀, Cop. Cop. in spring) the larvae were extremely mobile, all of them intensely protruding their embrional hooks in search of a point of adhesion (Kisielewska, 1955—56). If some of them were removed with faeces they were alive and very active. Probably they failed to get adhered to the intestine quickly enough. Larvae were often found which reached the body cavity only close to the anus in the abdominal part. That means that up to the last moment they did not lose their activity and did not stop trying to get adhered to the intestine although the peristaltic motion of the intestine forced them towards the anus. In such host species loose embryonal hooks were not found in the faeces if the culture of eggs had been fresh, i. e. larvae were not digested at all.

In diametrically opposed cases, e. g. *Cyclops vicinus* ♀♀ in winter and spring, *Acanthocyclops viridis* ♀♀ in autumm and winter, the majority of the swallowed larvae, or even all of them, were either killed by digestive juices and removed whole but dead in faeces or digested — in the latter case a great number of loose

embryonal hooks were found in faeces. Only very few larvae reached the body cavity.

In still other host species the condition was intermediate. Part of the larvae were digested, killed or stupefied as it were in the intestine, while the other part normally reached the body cavity. The larvae were often alive and even made weak movements, too weak however to enable them to get inside the body cavity. The quantitative relation of digested, killed or weakly moving larvae to the number showing normal activity differed depending on the host species and the season in which the invasion occurred. This was probably due to the degree of adaptation of *D. lanceolata* larvae to a given host species and depended on the individual resistance of the larvae and perhaps on the condition of the host.

(4) The speed and course of development of larvae in the body cavity of host.

It was proved that the development of the larvae in the body cavity of an obligatory host, e. g. *Cyclops strenuus strenuus,* in spring and summer and at room temperature from the moment of the entry of the oncospheres into the body cavity down to the formation of cercocysts took 9 to 11 days (K i s i e l e w s k a, 1955—56, 1957a).

Later investigations showed that cercocysts might form as soon as the eighth day. Some shorter or longer delay in comparison to the above mentioned optimum speed of development was observed however in some host species (e. g. *Cyclops strenuus strenuus* Cop. in winter and autumn, *Macrocyclops albidus* ♀♀, ♂♂ in winter and autumn, *Eucyclops serrulatus s.* str. ♀♀ in autumn, winter and spring). Larvae reached the form of cercocysts between the 10th and 18th days from the moment of invasion. An even longer delay in development was observed in *Eucyclops speratus* whose cercocysts developed between the 18th and 34th days from the moment of invasion. Moreover the phenomenon of completely checked development or death of larvae in various stages of their development was also observed in these hosts (K i s i e l e w s k a, 1957, b), as a result of which cercocysts did not form at all. Checked development or death might occur in a whole population of larvae (e. g. in *Cyclops furcifer* ♀♀ in spring, in *Acanthocyclops viridis* ♀♀ in winter) or its part (e. g. in *Cyclops strenuus strenuus* Cop. Cop. in autumn, in *Acanthocyclops viridis* ♀♀ in spring, in *Eucyclops serrulatus* s. str. ♀♀ in autumn, winter and spring). (Table I).

As the speed of development of *D. lanceolata* larvae depended to a large extent on temperature (Potiomkina, 1938; Kisielewska, 1955—56) individual cultures of invaded hosts were kept at the same temperature (18—22°) in order to standardze the conditions of the experiment.

(5) The system of intra-population relations.

It was found that the strength of the population exceeding 7 to 10 larvae in the obligatory host brought about the differentiation of the speed of development (the first group of the cercocysts developed in 9 to 11 days, a speed characteristic of uncongested populations, while the other larvae developed after a longer delay — Kisielewska, 1957).

In some host species these relation were somewhat modified: (a) the differentiation in the speed of development occurred in populations of less than 7 to 10 larvae, (b) the phenomenon of completely checked development or death of larvae occurred which could not result from the congestion of the population (Kisielewska, 1957, b). Thus, e. g. in *Acanthocyclops virdis* (in spring the differentiation in the speed of development of the population occurred when there were 3 to 5 larvae, while the death of larvae occurred seldom with the strength of the population greatly varying (17, 4, 7, 9, 2). In *Eucyclops serrulatus* s. str. even two or three larvae in the body cavity developed at a varying speed in spring, while death occurred fairly frequently with the strengths of the populations also varying.

Types of „*D. lanceolata* larvae — *Copepoda*" systems

All of the above mentioned criteria were characteristic of certain host groups in various seasons and interrelated. They made it possible to distinguish four basic types of „host-parasite" systems for *D. lanceolata* larvae and their hosts — *Copepoda*. These were: obligatory system, auxiliary system, accidental system and spurious system.

The obligatory system (systema obligatorium)

Considerable extensity of invasion (about 100%), high intensity of invasion (up to anything under twenty or a hundred larvae in the body cavity). All larvae in the body cavity of the host mobile, passing in great numbers to the body cavity; alive if removed. Speed of development varying from 8 to 11 days for all larvae, or for the first group of larvae in congested populations. Differentia-

tion of development speed appearing only in populations of 7 to 10 larvae. In congested populations all larvae standing a chance of reaching, although with some delay, the form of cercocysts if the life of the host was long enough. Death or completely checked development not observed. Of the *Copepoda* species we examined the following from the obligatory system with *D. anceolata* larvae: *Cyclops strenuus strenuus* ♀♀, ♂♂, Cop. Cop. V and IV in spring and summer, *Mesocyclops leuckarti* ♀♀ in spring and summer, *Acanthocyclops bicuspidatus* ♀♀, Cop. Cop. in spring and summer, *Acanthocyclops viridis* ♂♂ in spring, ♂♂, and Cop. Cop. in summer.

The auxiliary system (systema auxiliare)

Extensity fairly high, below 100% on the whole, intensity of invasion varying, generally lower than in the obligatory system. The majority of larvae in the intestine mobile and active, single specimens rarely removed in the condition of weakened mobility. Development speed varying from 8 to 11 days, yet development may also take longer. Intrapopulation relations similar to those in the obligatory system. Checked development or death not observed either. The following host species belong here: *Macrocyclops albidus* Cop. Cop. in autumn and winter, *Mesocyclops leuckarti* ♀♀ in winter, *Acanthocyclops bicuspidatus* ♀♀ in winter, *Acanthocyclops viridis* ♀♀ in summer, *Eucyclops macrurus* ♀♀ in spring and *Cyclops strenuus strenuus* Cop. Cop. III in summer.

The accidental system (systema accidentale)

Extensity from a few to a few tens of per cent, intensity very low, a certain percentage of larvae in the intestine getting digested and only a part passing to the body cavity. Development speed varying, tending to long delays. Differentiation in development speed occurring with the strength of the population being 3 to 5. Larvae may die or be completely checked in development. Species which may be assigned here are the following: *Cyclops strenuus strenuus* ♀♀, ♂♂, Cop. Cop. IV and V in autumn and winter, *Macrocyclops fuscus* ♀♀ in autumn and winter, *Macrocyclops albidus* ♀♀, ♂♂ in autumn and winter and ♀♀ in spring, *Acanthocyclops viridis* ♀♀ in autumn, ♂♂, Cop. Cop. in winter and ♀♀ Cop. Cop. in spring, *Eucyclops serrulatus* ♀♀ in autumn, winter and spring, *Eucyclops macrurus* and *Eucyclops macruroides* ♀♀ in

autumn and winter, *Eucyclops speratus* ♀♀, ♂♂ in winter, *Cyclops vicinus* ♀♀ in spring and *Acanthocyclops vernalis* ♀♀ in summer.

The spurious system (systema spurium)

Extensity and intensity very low; a large percentage of larvae in the intestine digested or killed and only single specimens passing to the body cavity. Whole populations die or are checked in development in the body cavity and, conseqently, in spite of single larvae reaching the body cavity, the cycle cannot be closed. The following species belong here: *Cyclops furcifer* ♀♀ in spring, *Acanthocyclops viridis* ♀♀ in winter.

Discussion

Two terms, „obligatory host" or „principal host" have come into use for describing a host which favours the development of the parasite. The latter term seems to be justified when it refers to ecological relations and not phenomena of physiological specificity. The principal host of a parasite in a given area (e. g. a given body of water), i. e. a host playing the most important part in the circulation of the parasite in a given biocoenosis, may be a species far from being physiologically best adapted to performing the function of a host. Its organism creates adequate but not necessarily optimum conditions for the development of the parasite. It plays however the role of a principal host because it occurs in great numbers and is a dominant in a given area. The term „obligatory system" as we use it is to render the physiological character of the „host--parasite" relation.

The term means that a host species forming an obligatory system with *D. lanceolata* larvae creates in its organism optimum conditions both for invasion (the habitat of the intestine) as well as for the development of the parasite (body cavity). To quote a few examples: *Cyclops strenuus strenuus* is an experimentally established obligatory host of *D. lanceolata* larvae in spring and summer, *Eucyclops macrurus,* as a dominant, is the principal host of these larvae in the area of the Żukówek goose farm, while *C. strenuus strenuus,* occurring in small numbers there, plays a minor, auxiliary part in the circulation of *D. lanceolata.* It may be supposed that in a body of water where *C. strenuus strenuus* would be a dominant it would play the part of the principal host and be

the obligatory host at the same time. The above example shows that physiological terms are not always synonymous with terms denoting ecological relations.

The terms „auxiliary system" and „accidental system" have been accepted for a long time and it seems to us that they may be synonymous in terms of physiological and ecological phenomena.

The term „spurious system" is quite new in the meaning with which we suggest to invest it. The distinction of this system is quite justified in the case of *D. lanceolata* larvae, but this system may not occur at all in the case of many other parasites (larvae or adult forms) and their hosts. The introduction of the term „spurious" is justified from the point of view of our material by the fact that in spite of the invasion (the entrance of larvae into body cavity) whole populations die or are completely checked in development at the stage of oncosphere, and cercocysts do not form at all. From the practical point of view the species forming a spurious system with *D. lanceolata* larvae play no more important part in the circulation of these parasites than the species which do not get invaded at all.

Remarks on the variability of „*D. lanceolata* larvae — *Copepoda*" systems

Thus, in the course of our investigations we met four modifications of relations between a given form of a parasite and its host. Yet an attempt at assigning permanently certain host species to definite systems showed that such classification could not be made in a stereotype and rigid way. To begin with, there are practically no distinct boundaries between the systems neighbouring in the list. It is particularly difficult to distinguish, in particular cases, between the obligatory and auxiliary systems and between the accidental and spurious systems, because some features, characteristic of both of these systems happen to combine in one host species and form an intermediate type as it were. For instance: *Eucyclops serrulatus* s. str. (♀ ♀) contacted with *D. lanceolata* eggs in spring (1956) got invaded in 32.6%, the mean intensity was 4.1 larvae, a certain percentage of larvae changed into cercocysts, the remaining larvae were checked in development or died. It might be said then that *E. serrulatus* (♀ ♀) formed a typical accidental system with *D. lanceolata* larvae. It appeared however that out of the

40.3% of invaded specimens showing mortality of larvae, 18.6%, or almost a half, were specimens in which whole populations died. These specimens were therefore spurious hosts. The same phenomenon although in different proportions was observed in young *Cyclops strenuus strenuus* invaded in autumn. In spite of that we included both the above mentioned species in the accidental system (in some seasons). It seems that individual features of both, host and parasite, are responsible for these and similar deviations. It may be supposed that examination of the invasional capacity of cercocysts formed in various hosts would complicate the picture of relations between the host and the parasite still further. The spurious system might then include also such hosts in which cercocysts develop but are unable to dominate the final host, i. e. are not invasional.

Table II

Invasion of larvae of *D. lanceolata* in copepodites of *C. strenuus strenuus*

Age of copepodites	No. of examined	Extensity	Intensity		Speed of develop.
			total	average	
Cop. V	39	100%	9—38	21.9	8—9 days
Cop. IV	24	100%	6—29	19.7	9—12 „
Cop. III	17	100%	1—8	2.7	14—18 „

The variability of relations between the host and the parasite which depends on physiological and phenological factors is another reason which makes it impossible definitely to classify concrete host species as components of definite types of systems. On the basis of our material we succeeded in establishing the following reasons for this variability: sex of the host, age of the host, and the season in which the systems form. Intensity and extensity of invasion and the conditions prevailing in the intestine connected with them the speed of development, and less frequently, the dying of larvae are the most labile features.

On the basis of the material which was available to us we can only say that the age and sex of the host in some cases had a decisive influence upon the differences in the course of the invasion and the deve-

Table III

Seasons	Obligatory system	Auxiliary system	Accidental system	Spurious system
Autumn		*Macrocyclops albidus* Cop.	*C. strenuus strenuus* ♀♀, ♂♂, Cop. IV, V; *Macrocyclops fuscus* ♀♀; *Macrocyclops albidus* ♀♀, ♂♂; *Acanthocyclops viridis* ♀♀; *Eucyclops macrurus* ♀♀; *E. macruroides* ♀♀; *E. serrulatus* s. str. ♀♀; *E. speratus* ♀♀, ♂♂	
Winter		*Macrocyclops albidus* Cop.; *Mesocyclops leuckarti* ♀♀; *Acanthocyclops bicuspidatus* ♀♀	*C. strenuus strenuus* ♀♀, ♂♂, Cop. IV, V; *Macrocyclops fuscus* ♀♀; *M. albidus* ♀♀, ♂♂; *Acanthocyclops viridis* ♂♂, Cop.; *Eucyclops serrulatus* s. str. ♀♀; *E. macrurus* ♀♀; *E. macruroides* ♀♀	*Acanthocyclops viridis* ♀♀
Spring	*Cyclops strenuus strenuus* ♀♀, ♂♂, Cop. IV, V; *Mesocyclops leuckarti* ♀♀; *Acanthocyclops bicuspidatus* ♀♀; *Acanthocyclops viridis* ♂♂	*Eucyclops macrurus* ♀♀	*Macrocyclops albidus* ♀♀; *Acanthocyclops viridis* ♀♀, Cop.; *Eucyclops serrulatus* s. str. ♀♀; *Cyclops vicinus* ♀♀	*Cyclops furcifer* ♀♀
Summer	*C. strenuus strenuus* ♀♀, ♂♂, Cop. IV, V; *Mesocyclops leuckarti* ♀♀; *Acanthocyclops bicuspidatus* ♀♀; *Acanthocyclops viridis* ♂♂, Cop.	*Acanthocyclops viridis* ♀♀; *C. strenuus strenuus* Cop. III	*Acanthocyclops vernalis* ♀♀	

lopment of larvae (e.g. in the case of *Cyclops strenuus strenuus* young and adult forms in autumn and spring, *M. viridis* ♀♀ and ♂♂ in winter and spring). Very distinct differences in the course of the invasion and in the speed of the development of larvae were observed in young *Cyclops strenuus strenuus*. These data are based on a rich material of *Copepoda*, differentiated into forms of the 1st, 2nd and 3rd stage, which was at our disposal in August 1956. The differences between these forms are shown in Table II. Now, as far as the influence of the season is concerned upon the variability of the „host-parasite" systems the material was sufficiently large for us to discuss this phenomenon in greater detail.

It was found in the course of the experiments that the same cyclops species behaved in a different way as hosts of *D. lanceolata* larwae, i.e. formed different types of systems with these larvae depending on the season in which they were invaded (Table III).

Cyclopes used for invasion were each time specially caught and not just taken from aquarium cultures. Thus planktin of spring generations was used in spring, that of autumn generations in autumn, etc. The same host species showed differences in the intensity of invasion and in the course of larval development in various seasons of the year. Owing to the complexity of these phenomena we cannot, at least in reference to *D. lanceolata* larvae, speak of obligatory or non-obligatory hosts in the absolute sense of the terms. We may however say that a certain host species (of a certain sex and age) forms with a certain parasite species an obligatory or some other system in a certain season. Moreover, if investigations are made in the field it seems necessary to determine the particular biocoenosis.

The influence of the season of the yeau unpon „host-parasite" systems is not probably the same in every combination of components as it is in the case of *D. lanceolata* larvae. It may be supposed that it depends on whether there are any regular cycles in the individual development of the parasite related to a season and on whether and to what extent the host itself (intermediate or final) depends in its way of life on the seasons of he year. Both these dependencies are there in the case of *D. lanceolata*.

Because of the way of life of geese as domestic water birds the circulation of *D. lanceolata* in natural conditions is connected with seasons. Geese go out to swim early in spring and infest the body of water with eggs removed with faeces. During the whole spring, summer and autumn until the body of water freezes geese infest it

and themselves get invaded through its plankton. Only the period of frosts constitutes a break in this constant exchange of invasions between the body of water and the geese feeding in it. Adult forms of *D. lanceolata* show some adaptation to the cycles described above. The following was observed at post-mortem examinations of, and while worms were removed from, 534 geese in various seasons during three and a half years: (1) distinct intensification of oviposition growing from spring to summer (maximum), (2) the phenomenon of destrobilation and failure to form proglottids with mature eggs in them late in autumn and in winter, (3) in addition to mature tapeworms numerous young ones were found in the intestines of geese in spring, summer and early autumn, which testified to a continuous new invasion in that period; no young strobiles were found in winter at all. If these data are compared with the phenomenon of the variability of the systems of larvae and cyclopes depending on the season of the year, it will be seen that it is precisely in autumn and winter that the greatest number of *Copepoda* species form with *D. lanceolata* accidental and spurious systems, while the number of obligatory and auxiliary systems grows in spring and summer (Table III).

It may be generally accepted that the spring and summer *Copepoda* generations get more heavily invaded and create better conditions in their body cavity for the development of *D. lanceolata* larvae than the autumn and winter generations of the same species.

The effect of the presence of *D. lanceolata* larvae on the hosts

If we discuss the „host-parasite" system as an ecological unit, we should take into consideration not only the influence of the host on the parasite but also the effect of the parasite upon the host, which characterizes in some measure the type of the system.

There are some data on the pathogenic action of *D. lanceolata* larvae and some other *Hymenolepididae* larvae. Paruchin (1954) found that cyclopes invaded with 5 to 10 *D. lanceolata* larvae died in 8 to 15 days from the moment of invasion, while if invaded with one larva they lived up to a month and a half. This author invaded cyclopes with eggs of various *Hymenolepididae* species and found that in the case of a heavy invasion by various species hosts die quickly, most frequenty during the period of morphogenesis or immediately after the invagination of the scolex. Further on Paruchin came to the conclusion that heavier invasions were not found in natural conditions because the more invaded cyclops died before or immediately after the formation of cercocysts in their body cavity.

While analysing the effect of *D. lanceolata* larvae upon hosts we took into account the following aspects: (a) the survival rate of cyclopes in individual cultures and the number of larvae in their body cavity, (b) in which development stage of the larvae the most intense mortality of cyclopes was observed.

Table IV

Survival of cyclopes in relation to the numerousity of larvae

Numerousity of population	Survival of cyclopes	
	average	limit
without larvae	38.6 days	27—48 days
1 larva	20.6 „	8—49 „
2 „	19.5 „	7—41 „
3 „	18.5 „	7—32 „
4 „	19.4 „	6—38 „
5 „	15.6 „	6—26 „
6 „	16.1 „	7—31 „
7 „	13.7 „	7—22 „
8 „	14.1 „	7—24 „
9 „	14 a. 19 „	—
10 „	15.3 „	5—21 „
11—16 „	12.2 „	9—18 „
17—25 „	9.8 „	7—13 „
over 26 „	8.1 „	4—11 „

It was found on preliminary examination that cyclopes of autumn and winter generations (irrespective of invasion) have a higher average survival rate than cyclopes living in spring and summer, and that various cyclops species live in individual cultures for a longer or shorter time on the average depending on their life requirements (e.g. oxygenfilous species live shorter as a rule than the benthonic ones which require less oxygen). In spite of the differences mentioned above the influence of the presence of larvae on the survival proved to be a feature dominant in so far as all species in all seasons could be considered jointly when results of the experiments were being established.

Table IV shows the survival rates of cyclopes in relation to the number of larvae in their body cavity. It follows from this table that sterile cyclopes kept in an individual culture live longer on the average than the invaded ones, and that the strength of the population of

the larvae does not fail to affect the host's lifetime. At the same time even if populations were numerous the lifetime of some, if not all, cyclopes was long enough for at least the first group of larvae to transform into cercocysts (K i s i e l e w s k a, 1957, a).

P a r u c h i n's suggestion was that the period of morphogenesis in the development of larvae generally causes the death of the host. Our research also showed that larvae exploit their environment most intensely in this period (K i s i e l e w s k a, 1957 a). The investigation made by M i c h a j ł o w (1958) on the symbiosis of larvae of *D. lanceolata* and *Triaenophorus lucii* also proved that *D. lanceolata* larwae in the period of morphogenesis made the development of *T. lucii* (M ü l l.) larvae almost completely impossible.

Of the total of the invaded cyclopes (100%) 53.7% of hosts die at the time when all or the first group of larvae have already transfomed into cercocysts and the remaining cyclopes (46.3%) die at the time before the larvae living in them succeeded in transforming into cercocysts. Whith the second group accepted as a whole (100%), 5.1% of cyclopes die with larvae in the form of oncospheres, 40.6% so with forms with a border, and 54.3% with larvae in the stage of morphogenesis. Consequently, the period of the parasite's morphogenesis really seems to be the most difficult for the survival of the host.

To sum up — *D. lanceolata* exerts a certain negative effect upon the host, not so great however as to render the development of a part of the larvae completely impossible.

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STRESZCZENIE

Praca niniejsza stanowi próbę klasyfikacji form stosunków zachodzących między larwami *Drepanidotaenia lanceolata* (Bloch) a ich żywicielami *(Copepoda)*, czyli próbę klasyfikacji układów „żywiciel-pasożyt" na konkretnym przykładzie.

1) Wyróżniono cztery zasadnicze typy układów „larwy *D. lanceolata* — *Copepoda*": układ właściwy (systema obligatorium), układ pomocniczy (systema auxiliare), układ przygodny (systema accidentale) i układ pozorny (systema spurium).

2) Oparto się przy tym na następujących kryteriach: ekstensywność inwazji, intensywność inwazji, zachowanie się larw w jelicie żywiciela (odporność na soki trawienne), tempo i przebieg rozwoju w jamie ciała żywiciela (tempo powstawania cerkocyst, zjawiska zahamowania w rozwoju, oraz obumierania larw), układ stosunków wewnątrzpopulacyjnych.

3) Stwierdzono, że w praktyce trudno jest zaszeregować w sposób bezwzględny poszczególne gatunki żywicieli do określonego układu, ponieważ: a) w obrębie jednego gatunku żywiciela panuje pewna (ograniczona zresztą) zmienność w układzie stosunków między poszczególnymi osobnikami żywicieli i larwami, wynikająca prawdopodobnie z właściwości indywidualnych zarówno żywicieli jak i pasożytów, b) zaznacza się wyraźne zmienność układów „żywciel-pasożyt" w obrębie jednego gatunku żywiciela, w zależności od jego płci i wieku, a zwłaszcza od pory roku w jakiej dany układ powstaje.

4) Stwierdzono, że w okresie wiosenno-letnim, kiedy w warunkach naturalnych odbywa się intensywne krążenie *D. lanceolata* w biocenozie (między środowiskiem wodnym, żywicielami pośrednimi i ostatecznymi) znacznie większa liczba gatunków *Copepoda* tworzy z larwami *D. lanceolata* układy właściwy i pomocniczy (a mianowicie: *Cyclops strenuus strenuus* Fischer ♀♀, ♂♂ Cop. IV i V, *Mesocyclops leuckarti* Claus ♀♀, *Acanthocyclops bicuspidatus* (Claus) ♀♀, *Acanthocyclops viridis* Jurine ♂♂ (wiosna) i Cop. Cop. (lato), *Eucyclops macrurus* G. O. Sars ♀♀ (wiosna)), niż to ma miejsce w okresie jesienno-zimowym, kiedy panuje przewaga liczbowa układów przygodnego i pozornego (a mianowicie: *Cyclops strenuus strenuus* Fischer ♀♀, ♂♂ Cop. IV i V, *Macrocyclops fuscus* (Jurine) ♀♀, *Macrocyclops albidus* (Jurine) ♀♀, ♂♂, *Acanthocyclops viridis* Jurine ♀♀ (jesień), ♂♂, Cop. Cop. (zimą), *Eucyclops serrulatus* s. str. Fischer ♀♀, *Eucyclops macrurus* G. O. Sars ♀♀, *Eucyclops macruroides* (Lillieb) ♀♀, *Eucyclops speratus* Fischer ♀♀, ♂♂). Tak więc te same gatunki żywicieli mogą spełniać różną rolę jako żywiciele pośredni *D. lanceolata* w różnych porach roku.

5) Stwierdzono, że obecność larw *D. lanceolata* wywiera pewien ujemny wpływ na żywicieli. Wyraża się on w tym, że średnia przeżywalność żywicieli w hodowlach indywidualnych jest niższa przy większych liczebnościach populacji pasożytów, przy czym okresem, w którym larwy najbardziej eksploatują żywiciela, wydaje się być okres morfogenezy. Ten ujemy wpływ nie jest jednak tak duży aby uniemożliwiał w ogóle rozwój larw.